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TAXONOMY OF THE STRIPE-HEADED TANAGER, GENUS *SPINDALIS* (AVES:THRAUPIDAE) OF THE WEST INDIES

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ABSTRACT.—The systematics of the genus *Spindalis* of the Greater Antilles and Cozumel Island, off Yucatan, are herein analyzed. Meristic data, coloration, and weight of the eight described taxa are compared. A table with extremes and means of all measurements is provided. Vocalizations of most of the principal taxa are compared. Final analysis of these comparisons suggests that rather than representing a single polytypic species, this complex is a superspecies with four allospecies: *zena*, *portoricensis*, *dominicensis*, and *nigricephala*. Therefore the Jamaican population becomes an endemic species, *Spindalis nigricephala*, as does the Puerto Rican *S. portoricensis*. Hispaniola and Gonave Island are inhabited by *S. dominicensis*. The fourth allospecies, *S. zena*, is a polytypic species represented by five endemic subspecies: *S. z. zena* in some islands of the Northern and Central Bahamas; *S. z. townsendi* confined to Grand Bahama, the Abacos, and Green Turtle Cay; *S. z. pretrei* in Cuban territory; *S. z. salvini* confined to the island of Grand Cayman; and *S. z. benedicti* confined to Cozumel Island, east of the Yucatan Peninsula, Mexico. A zoogeographic comparison with other endemic West Indian genera is presented. Received 11 June 1996, accepted 1 May 1997.

RESUMEN.—El presente trabajo analiza la situación sistemática de los ocho táxones del género *Spindalis* en las Antillas y en la isla de Cozumel, tomando en consideración las diferencias morfológicas (medidas, patrón, peso, diseño y coloración) en ambos sexos, resumidas en una tabla con sus medias y extremos. Una comparación de sus vocalizaciones es también expuesta, con sonogramas de algunos de los principales taxones. El resultado de estas comparaciones sugiere que no estamos en presencia de una especie politépica, sino de una superespecie con cuatro aloespecies bien diferentes: *zena*, *portoricensis*, *dominicensis* y *nigricephala*, por lo tanto la población de Jamaica está representada por una especie endémica, *Spindalis nigricephala*, al igual que Puerto Rico con *Spindalis portoricensis* y *Spindalis dominicensis* en Santo Domingo, incluyendo la Isla de Gonave. La cuarta aloes-

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pecie. *Spindalis zena*, es una especie politípica, representado por cinco subespecies endémicas: *Spindalis zena zena*, presente en algunas islas del norte y centro de las Bahamas; *S. z. townsendi*, confinada a las islas Abaco y Grand Bahama y a Green Turtle Cay, del norte de las Bahamas; *S. z. pretrei*, representada en el territorio cubano; *S. z. salvini*, confinada a la Isla de Gran Caymán, y *S. z. benedicti*, confinada a la isla de Cozumel, al este de la península de Yucatán. Se especula sobre el presunto aislamiento geográfico de estas poblaciones, así como se correlaciona el género *Spindalis* con otros géneros representados en las Antillas que pueden constituir presuntas de formas vicariantes.

The genus *Spindalis* Jardine and Selby, 1837, comprising the Stripe-headed Tanagers, is endemic to the Greater Antilles; a peripheral population on Cozumel Island, east of the Yucatan Peninsula, is part of the West Indian element in that island's fauna (Bond 1936). The relationship of *Spindalis* to mainland genera of tanagers is, to say the least, unclear. Three modern lists (Hellmayr 1936, Storer 1970, Sibley and Monroe 1991) agree in placing *Spindalis* between *Thraupis* and *Ramphocelus*. It is doubtful that this sequence is based on any critical study, as it has been repeated consistently since Sclater's "Synopsis Avium Tanagrinarum" (1856–1857), in which the classification was based in large part on differences in bill shape. Storer (1970, followed by Isler and Isler 1987) suggested a relationship between *Spindalis* and *Thraupis bonariensis* of southern South America. The lack of blue (conspicuous in all *Thraupis* except *T. palmarum*) in the plumage of *Spindalis* and the remoteness of the range of *T. bonariensis* from that of *Spindalis* makes such a relationship unlikely. In many ways, the plumage pattern of the Bananaquit (*Coereba*) resembles that of *Spindalis* more than does that of *T. bonariensis*, although this is not suggested as an indication of close relationship. It can be safely stated that the true relationship of *Spindalis* to mainland tanagers has yet to be determined.

Bryant (1866) proposed splitting the genus *Spindalis*, introducing the generic name *Spizampelis* for the group of taxa comprising the forms *pretrei*, *zena*, and *nigricephala*. This proposal has never been accepted, and Ridgway (1902) placed *Spizampelis* in the synonymy of *Spindalis*.

The Stripe-headed Tanager, according to Hellmayr (1936), Bond (1956), and the 6th edition of the American Ornithologists' Union Checklist (1983), consists of a single polytypic species, *Spindalis zena*, with eight recognized subspecies. These taxa are: *S. z. townsendi* and *S. z. zena* in the Bahaman archipelago; *S. z. pretrei* in the Cuban archipelago, *S. z. salvini* on Grand Cayman Island; *S. z. dominicensis* in Hispaniola and Gonave Island; *S. z. portoricensis* in Puerto Rico, *S. z. nigricephala* in Jamaica, and *S. z. benedicti* on Cozumel Island, Mexico. All of these forms except *townsendi* were originally described as species. In addition

to these eight forms, five other names have been proposed: *stejnegeri* Cory (1891) for the island of Eleuthera in the Bahamas; *pinus* Bangs and Zappey (1905) for the Isle of Pines (now the Isle of Youth), Cuba; *exsul* Salvin (1885) for Cozumel Island; *bilineatus* Jardine and Selby (1837) for Jamaica; and *multicolor* Vieillot (1822) for Hispaniola and the Bahamas. The names *exsul* and *bilineatus* are objective junior synonyms of *benedicti* and *nigricephala*, respectively. According to Hellmayr (1936), *stejnegeri* "seems to be an individual mutant without geographical significance," and he synonymized this name with *zena*. As for *pinus*, Todd (1917) pointed out that the alleged color characters differentiating it from *pretrei* were based on seasonal differences, and size overlapped too much to warrant recognition of *pinus*.

Allocation of the name *multicolor* Vieillot (1822) is more complicated. In Vieillot's description he clearly confused, under one taxon, the birds from Hispaniola and the Bahamas, as he mentioned having seen both (Bryant, 1867). In his description of the male, the characters agree perfectly with the Bahaman bird (already described by Linnaeus as *zena*), as it is the only form in the entire complex with a black back. Hellmayr (1936) believed that the description of the female of *multicolor* was based on the Hispaniolan bird, and therefore listed "*multicolor*, part" in the synonymy of *dominicensis* Bryant. However, Vieillot's description of the female did not mention streaked underparts, which are typical of the Hispaniolan population. The description of the female matches those of the Bahamas, so that Hellmayr's allocation of Vieillot's description as divided between the synonymies of *zena* and *dominicensis* was erroneous, and *multicolor* Vieillot is a synonym of *zena*.

Some authors, such as Ridgway (1902) and Hellmayr (1936) have cited the original description of *dominicensis* as "Bryant 1866." This paper was part of the proceedings of the meeting of the Boston Society of Natural History in December 1866, but was not actually published until May 1867, so the latter date is the correct citation, as given by Wetmore and Swales (1931) and Bond (1956).

The number of species to be recognized in the genus *Spindalis* has been much debated. James Bond changed his mind several times on this question. In his first book (1936) on West Indian birds, he listed six species, with only *zena* as polytypic (i.e., including *townsendi*); he did not mention *benedicti* of Cozumel Island, which was extralimital. In 1945, he wrote "Although the forms of *Spindalis* are geographically representative of one another, it obscures their affinities to regard them all as conspecific. Bahaman and Cayman Island birds and the one extralimital race from Cozumel were probably derived from Cuba." In accordance with the latter statement, he included *townsendi*, *pretrei*, *salvini*, and *be-*

nedicti in *zena*, recognizing *dominicensis*, *portoricensis*, and *nigricephala* as full species, thus going from six to four species in the West Indies. In his 1956 check-list Bond again admitted only a single species, but wrote in a footnote "Perhaps a more satisfactory taxonomic treatment of the genus *Spindalis* would be the recognition of three species based primarily on the coloration of females (i.e., *S. zena*, *S. dominicensis*, and *S. nigricephala*)." Nevertheless he continued to admit only a single species as late as the fifth edition (1985) of his field guide. Other recent authors of regional works who have listed their resident form as a race of *Spindalis zena* include Garrido and García Montaña (1975), Dod (1978, 1981), Raffaele (1983), Bradley (1985), and Downer and Sutton (1990). In check-lists, Storer (1970) and the A.O.U. (1983) recognized only one species of *Spindalis*.

Steadman et al. (1980) compiled a table of weights of West Indian birds they had obtained in the field. They quoted Bond's 1956 statement suggesting the possibility of dividing *Spindalis* into three species based mainly on coloration of females, and went on to say "Our data on weights supports this treatment." This was based on their finding that Jamaican *Spindalis* weighed approximately twice as much as those from the Bahamas and Hispaniola. In their table they used the names *Spindalis z. zena*, *S. zena townsendi*, *S. portoricensis dominicensis*, and *S. nigricephala*. Differences in body weight alone should not be sufficient for species status, as there are no doubt several polytypic species in which the largest subspecies weighs twice as much as the smallest (the Song Sparrow, *Melospiza melodia*, comes to mind). Moreover, Steadman et al. did not have weights for *benedicti*, although these have been published by Paynter (1955). The weights given by Paynter exactly match those on labels of specimens in the Carnegie Museum of Natural History. At 26–36 gm, they fall midway between those of *nigricephala* and those of the smaller taxa, thus making the large size of *nigricephala* less striking.

If three species are to be recognized, there is disagreement as to their names. The A.O.U. (1983), although treating *Spindalis* as monotypic, repeated Bond's suggestion that the three should be *zena*, *dominicensis*, and *nigricephala*, but as indicated above, Steadman et al., used the species names *zena*, *portoricensis*, and *nigricephala*. They were correct insofar as nomenclature is concerned, as when Hispaniolan and Puerto Rican populations are combined into a single species, the name *portoricensis* Bryant, 1866, has priority over *dominicensis* Bryant, 1867. In addition to the AOU Checklist (1983), works that erroneously use the junior name *dominicensis* for the combined Hispaniolan and Puerto Rican populations include Bond (1956), Sibley and Monroe (1990), and its offshoot, Monroe

and Sibley (1993). The latter two works admit only a single species of *Spindalis*, but list "groups" recognized as species by some authors.

Amadon and Short (1976) introduced the term "megasubspecies" for "well-marked forms approaching the level of species, but nonetheless judged to be conspecific." One of their examples was the genus *Spindalis*, which they divided into five megasubspecies. One of these, *zena*, would consist of what they called "the minor subspecies *townsendi* and *zena* together." Unfortunately they used the erroneous name *multicolor* for the Hispaniolan "megasubspecies," and overlooked the Cozumel and Grand Cayman populations, *benedicti* and *salvini*. Their proposal has had little or no support.

Spindalis is a non-migratory West Indian genus, with the only extralimital race, *benedicti* of Cozumel Island, being an obvious derivative from one of the West Indian populations. Although larger than any of the members of the *zena* complex (Cuba, Bahamas, Grand Cayman), the resemblances in color of both males and females to members of that group strongly suggest that the affinities of the Cozumel Island population are with the *zena* complex. The resemblances of *benedicti* are a mosaic of the other members of that complex; nearest *townsendi* in back and upper breast color of males, nearest *zena* in nuchal collar and rump color of males, nearest *salvini* in intensity of yellow on throat and lower breast of males, and nearest *pretrei* in tail pattern of females.

The biological species concept is difficult to apply when dealing with allopatric populations, because there is no direct evidence for presence or absence of reproductive isolation (Mayr and Short 1970). Radiations of closely allied forms at uncertain levels of speciation have occurred in several West Indian groups, in amphibians and reptiles as well as in birds. Parkes (1991) has discussed the difficulties of assessing the taxonomic status of replacing forms in an archipelago, with special emphasis on the Philippines, but mentioning the *Spindalis zena* and *Tyrannus (Tolmarchus) caudifasciatus* groups as examples of problem groups in the West Indies. Vocalizations play an important role in the discrimination of mainland species, but differences in vocalizations among allopatric insular forms are not necessarily indicative of species status in the absence of other differences. However, when such differences are combined with morphological, ecological, or ethological differences, vocal evidence can be given great weight; such is the case in *Spindalis*.

The objective of the present study is to reexamine the members of the genus *Spindalis* in the light of the various opinions as to the number of species to be recognized.

MATERIALS AND METHODS

Garrido and Kirkeconnell examined 369 skins (253 males and 116 females) of *Spindalis*, housed in the following institutions: American Museum of Natural History, New York

TABLE 1
MEASUREMENTS (IN MM) OF *SPINDALIS* SP.^a

	Wing (flat) (except <i>nigricephala</i> = chord)			Tail		
	N	Range	Mean ± SD	N	Range	Mean ± SD
MALES						
<i>S. z. pretrei</i>	(42)	69–80	75.1 ± 2.493	(41)	51–61	55.6 ± 2.106
<i>S. z. salvini</i>	(18)	80.5–87	83.4 ± 1.739	(19)	56–65.5	62.4 ± 2.235
<i>S. z. benedicti</i>	(12)	79.5–86	82.0 ± 2.089	(11)	61–70	64.0 ± 2.485
<i>S. z. townsendi</i>	(26)	75–82	78.6 ± 2.232	(26)	54–65	59.7 ± 2.813
<i>S. z. zena</i>	(78)	72–84	77.8 ± 2.479	(76)	52–66	58.8 ± 2.718
<i>S. portoricensis</i>	(26)	82–88.5	85.2 ± 1.891	(26)	59–68	63.6 ± 2.244
<i>S. dominicensis</i>	(24)	80.5–93	85.8 ± 4.316	(24)	61–75	66.7 ± 3.863
<i>S. nigricephala</i>	(16)	94–103	99.6 ± 2.410	(16)	70–80	74.8 ± 3.194
FEMALES						
<i>S. z. pretrei</i>	(18)	68–75.5	72.0 ± 2.233	(18)	49.5–57	52.9 ± 2.002
<i>S. z. salvini</i>	(4)	78.5–83	80.4 ± 2.057	(4)	58–63.5	59.5 ± 2.677
<i>S. z. benedicti</i>	(9)	76.5–80.5	78.6 ± 1.424	(9)	55.5–61	59.1 ± 1.828
<i>S. z. townsendi</i>	(13)	72–76.5	74.3 ± 1.640	(13)	53–58	55.3 ± 1.186
<i>S. z. zena</i>	(27)	69.5–78	73.8 ± 2.206	(30)	52–58.9	54.9 ± 2.119
<i>S. portoricensis</i>	(12)	80–85.5	82.6 ± 1.649	(11)	56–65.5	60.6 ± 2.290
<i>S. dominicensis</i>	(21)	77–88	81.7 ± 3.164	(20)	55–66	61.6 ± 3.302
<i>S. nigricephala</i>	(11)	90–98.5	95.4 ± 2.548	(12)	67–76	72.3 ± 2.879

^a (N).

(AMNH); Royal Ontario Museum, Toronto; Institute of Jamaica, Kingston; Instituto de Ecología y Sistemática, Academia de Ciencias de Cuba; Universidad de la Habana, Cuba; and Museo Nacional de Historia Natural, Cuba. Data from these specimens were supplemented by 65 males and 33 females examined by Parkes in the Carnegie Museum of Natural History (CM); the series of *portoricensis* and *townsendi* were substantially larger than those available to the other authors. In order to study individual variation in *townsendi*, Parkes borrowed series from the Field Museum of Natural History (FMNH) and the Museum of Natural Science, Louisiana State University (LSU). Sutton obtained his data from banded birds. Table 1 presents available weights (in g) and the conventional measurements (in millimeters) of the wing (flattened), tail, tarsus, and exposed culmen. Egg measurements, also in millimeters, are taken from the literature. Vocalizations were recorded in Puerto Rico, the Dominican Republic, Cuba, Jamaica, and Grand Cayman by G. B. Reynard; in Puerto Rico by José Colón; in Jamaica and Grand Cayman by Robert Sutton; in the Bahamas by Paul Dean and P. P. Kellogg (Library of Natural Sounds [LNS], Cornell University collection); in the Dominican Republic by T. Parker III (LNS); and on Cozumel Island by R. B. Waide (also LNS). Tape recordings were made using several models of Nagra, Uher reel-to-reel types, and a Sony TM 5000 cassette recorder, usually with microphones in 61 or 91 cm parabolic reflectors. Sonograms were made using Kay Elemetrics equipment. Published recordings include those made by Reynard and his colleagues in Puerto Rico, Hispaniola, and Cuba (Reynard, 1969, 1981; Reynard and Garrido, 1988). Weights of birds were taken in Cuba by R. Piechoki, K. Uhlenhaut, O. Garrido, and A. Kirkconnell; in Puerto

TABLE 1
EXTENDED

Culmen			Tarsus		
N	Range	Mean \pm SD	N	Range	Mean \pm SD
(37)	10.1–13.1	11.0 \pm 0.727	(38)	17.5–23	20.1 \pm 1.380
(19)	10.1–12.5	10.7 \pm 0.561	(17)	19.5–22.6	21.3 \pm 0.946
(12)	12.8–14.7	13.8 \pm 0.744	(12)	19.5–23	21.1 \pm 1.296
(25)	10.4–12.9	11.7 \pm 0.695	(26)	18.8–23.5	20.7 \pm 1.234
(78)	9.6–13.8	11.2 \pm 0.709	(76)	18.5–23.5	20.7 \pm 1.049
(25)	10.4–13	11.7 \pm 0.605	(25)	19.5–23.5	20.7 \pm 1.037
(24)	8.7–10.8	9.7 \pm 0.575	(24)	18.5–23	20.7 \pm 1.070
(17)	10.4–13.5	12.4 \pm 0.905	(13)	21–24.5	22.2 \pm 1.140
(18)	9.7–12.2	11.0 \pm 0.727	(18)	17.4–21.2	19.7 \pm 1.167
(5)	10.3–11.5	10.6 \pm 0.546	(5)	20.5–23.8	21.4 \pm 1.374
(8)	10.7–13.7	12.2 \pm 1.370	(9)	20.5–22.8	21.2 \pm 0.918
(13)	9.7–11.2	10.5 \pm 0.514	(12)	18.2–21.7	20.5 \pm 1.159
(30)	9.1–11.4	10.4 \pm 0.500	(28)	18.5–23	20.9 \pm 1.183
(12)	10.7–12.3	11.5 \pm 0.504	(12)	19.5–23	21.1 \pm 1.135
(21)	7.6–10.1	8.9 \pm 0.697	(20)	19–23.5	21.4 \pm 1.551
(12)	10.1–15.1	12.4 \pm 1.213	(10)	21.5–23.2	22.4 \pm 0.549

Rico by Olson and Angle (1977); in the Cayman Islands by Olson et al. (1981); in the Bahamas, Hispaniola, and Jamaica by Steadman et al. (1980); in Jamaica by Robert and Ann Sutton; and in Cozumel Island by Paynter (1955) and Parkes (Table 2).

In coming to our conclusions, we have also consulted the data published by Ridgway (1902) and remarks on systematics of *Spindalis* by the several other authors cited in this paper.

Comparisons

Although Ridgway (1902), Hellmayr (1936), and Bond (1936) gave diagnostic characters and partial descriptions of all forms of *Spindalis*, they did not make full comparisons among all of them. We make such paired comparisons here. Suggestions for dividing *Spindalis* into several species have emphasized characters of females, but males also exhibit striking differences in color and pattern. For mensural characters, see Table 1.

I. The *zena* complex. This group has the following characters in common: females essentially olive green with no bright colors, unstreaked ventrally; males with nuchal collar and rump patch of various mixtures of chestnut and yellow; a chestnut band (brownish orange in some individuals of *pretrei*) across upper breast, separating the yellow of the throat

TABLE 2
WEIGHTS (IN GM) OF *SPINDALIS* SP.*

	N	Range	Mean	SD
MALES				
<i>S. z. pretrei</i>	19	18.5–25.5	22.0	1.62
<i>S. z. salvini</i>	16	20.5–31.0	23.1	1.54
<i>S. z. benedicti</i>	9	26.8–35.6	30.8	3.20
<i>S. z. zena</i>	11	19.2–23.2	21.1	1.36
<i>S. portoricensis</i>	109	22.5–37.0	30.8	2.82
<i>S. nigricephala</i>	111	38.0–64.8	43.0	0.20
<i>S. nigricephala</i> (Robbins)	29	38.0–54.1	44.7	3.53
FEMALES				
<i>S. z. pretrei</i>	12	18.0–25.0	22.4	2.07
<i>S. z. salvini</i>	8	24.0–28.5	25.5	0.31
<i>S. z. benedicti</i>	6	26.5–32.8	30.0	2.37
<i>S. z. zena</i>	7	17.0–25.5	21.7	2.58
<i>S. portoricensis</i>	42	28.0–41.1	33.5	3.30
<i>S. nigricephala</i>	48	45.2–53.7	47.2	**
<i>S. nigricephala</i> (Robbins)	6	38.0–50.7	44.0	4.38

* Adequate weight samples were not available for *S. z. townsendi* and *S. dominicensis*.

** SD not computed.

and that of the lower breast; tail black with varying amounts of white but always with outer and central rectrices edged in white.

1. *Pretrei* versus *salvini*: In males of *salvini* the color of the chest averages richer and is more extensive anteriorly, extending farther forward than in *pretrei*, reducing the size of the yellow patch on the lower throat. The white of the chin extends posteriorly between the black malar stripe and the yellow throat patch, further restricting the latter. In *pretrei* the white superciliary line is continuous, whereas in *salvini* it is broken by black or black-tipped feathers above the eye. Dorsally, *salvini* is slightly darker green on the mantle. The nuchal band is strongly bicolored—chestnut anteriorly and narrowly yellow posteriorly. In *pretrei* the division between chestnut and yellow is less clearly defined. The rump of *salvini* is chestnut, the feathers narrowly bordered with yellow; the anterior margin of the chestnut area is narrowly greenish yellow. The rump of *pretrei* is more orange, with a less distinct anterior border of yellow. Females are very similar; *pretrei* is slightly greener, less gray dorsally than *salvini*. The whitish malar stripe is more conspicuous and more clearly defined along its lower margin in *pretrei*. The white patch on the outermost rectrix

is more extensive anteriorly in *pretrei*. *Salvini* averages slightly larger than *pretrei* in all dimensions.

2. *Pretrei* versus *benedicti*: In males of *benedicti* the color richness seen in *salvini* goes even farther. The breast is much darker chestnut, becoming blacker anteriorly and blending with the posterior end of the black malar stripe. The yellow throat patch is restricted by the black malar stripe. The rump and nuchal band of *benedicti* are dark chestnut, with narrow yellow tips to some of the feathers. The green of the back is much darker with a brownish cast. In females, *benedicti* is very slightly darker green dorsally and on the breast than *pretrei*. The whitish malar stripe is obsolete, the throat being barely paler laterally than centrally. The amount of whitish in the inner webs of the outer two pairs of rectrices is variable but usually more than in *salvini* and less than in *pretrei*. *Benedicti* is the largest of the forms in the *zena* group, being somewhat larger than *salvini* and decidedly larger than the other forms. This is particularly conspicuous in the bill.

3. *Benedicti* versus *townsendi*: Males of these two forms are quite similar in color. The yellow of the underparts of *townsendi* is richer with a slight orange tinge. The chestnut on the breast of *townsendi* is almost as dark as in *benedicti*, but slightly less extensive. The green of the mantle of many *townsendi* is nearly identical with that of *benedicti*, although many *townsendi* have the dorsum washed with blackish, an approach to *zena*. The nuchal band and rump of *townsendi* are conspicuously bordered with yellow posteriorly and anteriorly, respectively; in *benedicti*, the margin of the chestnut is barely yellower than the mantle. Females are indistinguishable in color, separable only by size.

4. *Zena* versus *townsendi*: *Zena* is the only member of its group in which the mantle of males is black rather than greenish. This increase in melanin is also manifested in the black malar stripe, which is much wider than in any other form (except in some Bahaman specimens), restricting the yellow throat patch to a more linear shape and the chestnut of the breast to a central spot. The nape and rump are strongly bicolored, as in *townsendi*, but the chestnut averages darker and the yellow border narrower and more sharply defined.

Individual variation in *zena* is most noticeable in the underparts. The breast varies from entirely chestnut (the posterior feathers yellow-edged) to the chestnut being confined to a narrow transverse area just below the chestnut extension of the yellow throat patch. In many individuals, the yellow throat is mixed with chestnut; this is not necessarily correlated with the amount of chestnut on the breast. Neither of these characters is correlated with age; both extremes can be found in both age classes. The sides and flanks are olive-gray, as in the other subspecies of the *zena*

group, although perhaps slightly darker. However, this area is sometimes faintly streaked with black and occasionally heavily streaked (CM 30659, 1st year bird). Although the male of this subspecies is always characterized as having a black back, the dorsal feathers are occasionally inconspicuously and narrowly edged with orange-brown, being seen only in the hand and in good light (1 of a CM series of 6 from Blue Hills, Nassau, 30 December–15 January 1908–9).

Individual variation in males of *townsendi* is of particular interest, as it appears to exceed that found in any other subspecies. For this study, Parkes assembled an unprecedented series of 68 males from FMNH and LSU to supplement the 14 in CM. Of these 82, 45 were from Great Abaco (type locality of *townsendi*) and 37 from Grand Bahama.

The chestnut breast band is narrow and less variable in extent than in *zena*, from a slight extension of the chestnut throat area (FMNH 27703) to a relatively broad lateral extension much mixed with yellow (FMNH 27284), but never as extensive posteriorly as in extremes of *zena*. The yellow of the throat is seldom as intensely orange as in *zena*, although more-or-less streaked with chestnut in 24% of Abaco specimens examined. The width of the malar stripe and consequent restriction of the yellow throat area is variable, matching *zena* in this respect in some individuals.

The most variable area is the back. It ranges from unmarked greenish orange to black with dull orange feather edgings. This is not correlated with age. Those with the black extreme constitute 14 of 45 (31%) of the Abaco specimens. This variability was recognized by Ridgway (1887), who described *townsendi* from five males and three females from Abaco.

Males from Grand Bahama do not differ from Abaco birds except in back color. The black extreme is much less common on Grand Bahama. In the series examined, only three of 37 specimens (8%) matched the black individuals in the Abaco series. This difference may well be explained by a limited gene flow from the black-backed *zena*. Abaco is closer than Grand Bahama to New Providence, the nearest island inhabited by *zena* (and in fact its type locality). That *Spindalis* can move from island to island is demonstrated by Buden (1987), who stated that *zena* invaded Providenciales Island in the Caicos Islands (the nearest island to the southern Bahamas) in the 1970s.

Females of the two Bahaman forms are much more similar than the males. The ventral color is identical. Some individual females of *townsendi* may have almost imperceptible blackish shaft-streaks on the mantle; these are better developed in *zena*, in which the crown may also be faintly spotted with blackish.

II. *Nigricephala*. This is the most distinctive *Spindalis*, both in color and in size. It is the largest, weighing twice as much as the smallest form,

zena (Table 1). Males differ from all other forms in lacking yellow on the chin, which is white. In adult males, the broad black malar stripes merge across the upper breast; in first-year males the connection is narrower, the black being parted by an extension of the orange of the breast. There is no chestnut on the breast. Below the black, the breast is rich, glossy orange, and the yellow of the posterior underparts, unlike the members of the *zena* complex, extends all the way to the abdomen; only the under tail coverts and (in some) a few adjacent abdominal feathers are white. The back is purer green than in any of the *zena* complex, and there is, at best, only a faint trace of a nuchal band (see photograph on p. 122 of Downer and Sutton 1990). The rump varies from being merely a bit paler than the mantle to dull orange. The bend of the wing is black, lacking any trace of the chestnut patch found (in varying degrees of size and depth of color) in all other males of *Spindalis*. The narrow outer edgings of the remiges are yellowish in first-year birds, white in older males. White on the tail is confined to R6, the outermost rectrix (with an occasional trace at the tip of R5), and is much less extensive than in the *zena* complex.

The brightly colored females of *nigricephala* are unique in the genus *Spindalis*. The underparts, from the breast to the lower abdomen, are yellow, tinged with orange on the upper breast. The under tail coverts and a variable amount of the lowermost abdomen are grayish white. The throat is light neutral gray, contrasting sharply with the orange-yellow (and often a central bright orange area) of the upper breast. The chin, malar stripe and superciliary are indistinctly paler than the throat. The crown and nape are darker gray, washed with greenish in fresh plumage. With wear, the green overlay is lost, and, in some individuals, whitish shaft-streaks are revealed on the crown and ear coverts. The mantle is much greener than in any member of the *zena* complex, and only slightly darker than in males of *nigricephala*; as in the former, the rumps of females are brighter and yellower. White in the rectrices is confined to an edging on the terminal quarter of the inner web of R6 and, sometimes, a trace in the same area of R5. The tail and wings are blacker than in the *zena* complex, and the edgings of wing feathers whiter, thus almost as conspicuous as in males.

III. *Dominicensis* and *portoricensis*. The two remaining forms have one distinctive character in common; females and juvenile males have streaked underparts. Adult males, however, are quite different from one another. Comparisons with other forms are as follows.

1. *Dominicensis* versus the *zena* complex: In males the color and pattern of the underparts are quite similar to those of *salvini*, except that the yellow of the abdomen of *dominicensis* is richer and extends farther pos-

teriorly. Dorsally, however, *dominicensis* is unique. The mantle feathers are black at the base and tipped with yellow, giving a dark yellow-green effect. The nuchal collar is broader than in any other form and is brilliant yellow, with an orange tinge anteriorly. The rump color is much as in *salvini*, except that the yellow of the anterior margin is deeper and contrasts more with the mantle. The chestnut patch at the bend of the wing is the most extensive in the genus, including all but the tips (which are black) of the lesser coverts. As mentioned above, females differ from those of the *zena* complex in having narrow blackish streaks on the underparts; the base color is much as in *townsendi*. Dorsally, females of *dominicensis* are greener than any in the *zena* complex, and the rump is distinctly yellowish, contrasting sharply with the mantle. Males in juvenal plumage are heavily streaked ventrally with blackish streaks on a white background. Unlike adult females, they are also streaked dorsally, although the blackish streaks are inconspicuous against the dark green background. The rump is like that of adult females but with a slight chestnut tinge.

2. *Portoricensis* versus the *zena* complex: Definitively plumaged males differ from all of the *zena* group in several ways. At least in 19 CM specimens from west-central and eastern Puerto Rico (Utua, Adjuntas, Guayama, Fajardo) there is no trace of chestnut on the breast; instead, there is a small patch of bright, glossy orange feathers, similar to those of *nigricephala*, just posterior to the yellow throat (as shown on the color plate). F. Vilella (in litt.) states that he has seen males in western Puerto Rico with some chestnut on the breast, so there is at least the possibility of geographic variation in this character within Puerto Rico. The throat and the white chin are conspicuously spotted with black (some other races, such as *benedicti* and *townsendi*, may occasionally have a few tiny black spots on the throat). The yellow of the lower breast is greener than in any of the *zena* group. Even in definitively plumaged males, there are vague gray streaks on the whitish flanks. The green of the mantle is nearest that of *salvini*, but slightly darker. There is a narrow, bright orange nuchal collar, faintly tinged with chestnut at the anterior edge. Unlike all of the *zena* group, there is no contrasting rump patch; the rump feathers are merely a slightly brighter yellow-green than the mantle. First-year males are highly variable and differ from older males in being streaked with dark gray on the sides and flanks and even to some extent in the yellow of the breast. The yellow is less extensive posteriorly than in the older birds and is variable in extent. There is just a hint of the orange spot at the posterior border of the yellow throat patch. Dorsally, the two age classes of males are much alike, but in at least some of the younger birds, the mantle feathers have inconspicuous narrow black shaft streaks.

The rectrices of male *portoricensis* are unique. Rather than being black with a large white patch, as in all other *Spindalis*, they are dark olive brown, edged externally (when fresh) with yellowish green, like those of the female. White is confined to a narrow line on the outer margin of the inner web of the two outermost rectrices.

Females of *portoricensis*, like those of *dominicensis*, differ from the *zena* group in being streaked ventrally. As in males, there appear to be two age classes subsequent to the juvenal plumage. In what we take to be the younger birds, the streaks are somewhat blurred; the background color, although not pure white, is paler than in any member of the *zena* group. The mantle color is dark, as in *benedicti*, but greener and less gray, and, unlike *benedicti*, the rump is brighter green than the mantle (but not as much so as in *dominicensis*). There are a sharply contrasting white malar stripe and a narrow superciliary stripe similar in its development to that of *pretrei* but whiter. In older females the mantle is slightly brighter green, and there is a narrow greenish-yellow nuchal collar. The streaking of the underparts is more sharply defined than in the younger birds, and the breast is saturated with bright greenish yellow, tending toward orange anteriorly and continuing as a faint yellow wash back to the abdomen. The white malar stripe is equally prominent, but the superciliary stripe is obsolescent.

In summary, males (collectively) of the *zena* group (*pretrei*, *salvini*, *zena*, *townsendi*, *benedicti*) are characterized by having varying amounts of chestnut on the breast, rump, and nuchal collar (listed above in increasing sequence of chestnut pigmentation). Males of *dominicensis* have the chestnut of breast and rump developed about as in *salvini* but lack chestnut in the nuchal collar which is broad and brilliant orange-yellow. The mantle differs from all of the *zena* group in consisting of black feathers with yellow tips. Males of *portoricensis* lack chestnut entirely (except possibly on the breast in western Puerto Rico), have black-spotted throats, streaked flanks (especially in first-year birds), no contrasting rump-patch, and female-like rectrices. Males of *nigricephala*, in addition to their great size, are unique in lacking a nuchal collar and in having the throat white rather than yellow. They also lack a rump patch and any chestnut in the plumage.

The females of all of the *zena* group are slightly varying shades of greenish gray, scarcely if at all paler on the rump, and with no markings on body plumage except a tendency for whitish malar and superciliary stripes. Females and juveniles of *dominicensis* and *portoricensis* are unique in having streaked underparts; those of *dominicensis* differ in having the rump conspicuously brighter than the mantle. Females of *nigri-*

cephala, in addition to their great size, are unique in having brilliant yellowish underparts, strongly contrasting with their neutral gray heads.

Vocalizations

This group of tanagers is characterized by the high-pitched notes they emit, some at or above 8 khz. Songs can be difficult to detect because of their ventriloquial quality and because males may sing from the highest treetops. Females characteristically sing their “whisper songs” when hidden in dense thickets; one we recorded was less than 0.5 m above the ground. In the effort to characterize the songs assembled for this study, we lack the advantage of having any published full life history studies of any of the populations of *Spindalis* but hope our information will spur others to continue studies of this interesting genus!

Sound tapes described are from unpublished material in the Cornell Library of Natural Sounds, our new recordings, and from three publications covering Puerto Rico, Hispaniola, and Cuba (Reynard 1969, 1981; Reynard and Garrido 1988), respectively.

Prior to those published recordings, several authors had written subjective descriptions of *Spindalis* vocalizations. Bond (1936:369) generalized by writing: “with the exception of the Cuban and Bahaman species, which possess a prolonged but remarkably weak song, I have never heard them emit more than a shrill, drawn out *seep*.” Other published descriptions will be entered in the island by island discussion along with the analyses of vocalizations presented here.

Puerto Rico.—Wetmore (1927) wrote of the Puerto Rican birds: “The call-note is a faint “*tseet*”, and males give a low chattering note. I heard no song from them, but Danforth has recorded a weak though spritely effort heard very rarely.” On the other hand, according to Raffaele (1983), the Puerto Rican bird does sing: “Its thin, but distinctive song can be heard commonly during the breeding season *zeé-it-zeé-tittit-zeé*. The *zeé* syllable often seems like an inhaling sound. This basic call has many variations. A thin trill like the beating of a tiny hammer is rarely heard as is a short twittering call. The call note is a soft ‘*tewweep*.’ The distinctive principal call in our recordings (Fig. 1A) is a continuing series of high-pitched, thin, sibilant notes, given in a rhythmic pattern, much like that described by Raffaele, which we paraphrased as “*seet see seee seet see seee seet see seee*,” given repeatedly in groups of three of the 3-note phrases, two of which are shown in Fig. 1A. The short songs were separated by ca. 4 sec pauses.

Among other vocalizations recorded are a fast “*twitter*” (Fig. 1B) and a short “*chi chi chi*,” descending in pitch (Fig. 1C). Three intense, very high-pitched, squeaky “*lisps*,” resembling a “*tsee er*” phrase (Fig.

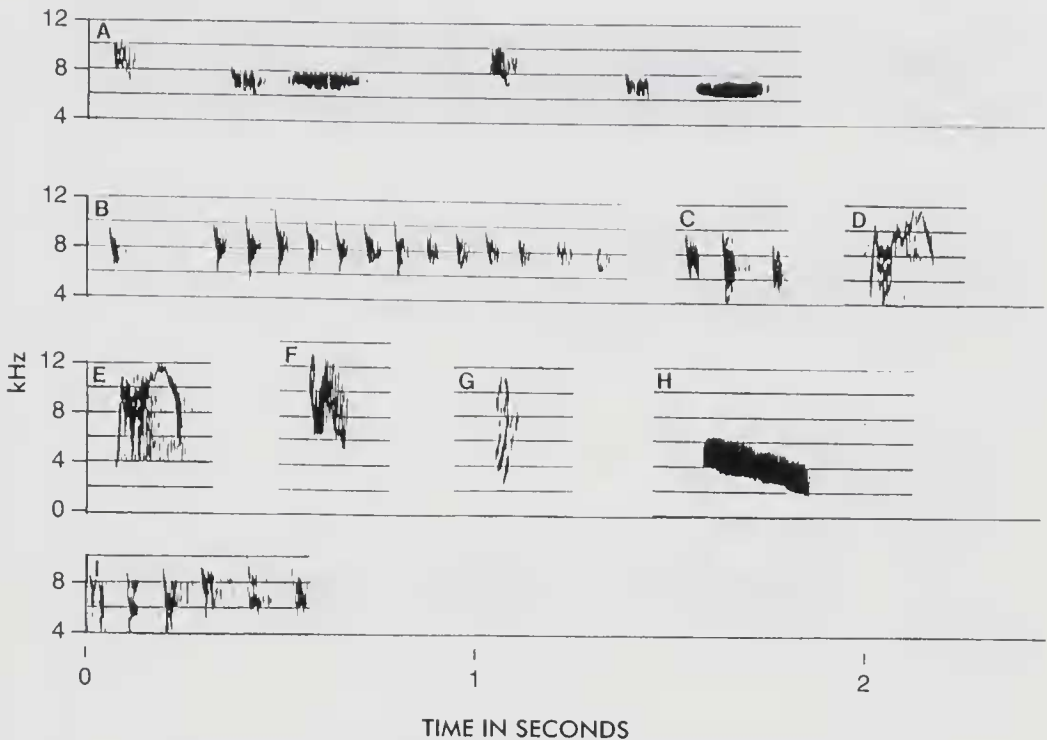


FIG. 1. Vocalizations of *Spindalis portoricensis* (see text).

1D,E,F) are probably aggression calls. An apparent “contact call,” during feeding sessions (Fig. 1G) is a “*queet*” sound, rapidly ascending in pitch. The descending whistle (Fig. 1H), of undetermined context, is lower in frequency than most other calls. A short, rapid chatter is a “fly-off” vocalization; it was accompanied by “clicks” from wing fluttering, which resulted in some of the vertical, faint lines in the sonogram (Fig. 1I).

Hispaniola.—Wetmore and Swales (1931) stated of Hispaniolan *Spindalis*: “They are very silent and seldom call, their note then being low and faint. Wetmore heard one utter a weak, sibilant song that may be written *tsee see see see*, in so low a tone that it was heard with difficulty, which agrees with Verrill’s notes that the song is feeble and insect-like” (Verrill and Verrill 1909).

The weak song referred to above is not in our collection of tapes, but consists of “seep” notes given more rapidly than those shown here (Fig. 2A), which were recorded during an introductory period before initiation of a song series. This is considered a territorial song.

The “twitter” (Fig. 2B) and the low-pitched double “churrs” (Fig. 2D) are believed to be conflict-related calls. A “whisper song” from a female (Fig. 2C) was typically weak, lacked evident rhythm, with ever-changing syllables, in a more or less recitative or conversational pattern. A heavy background chorus obscured the tanager voice in the original recording, so this is a tracing from the original sonogram.

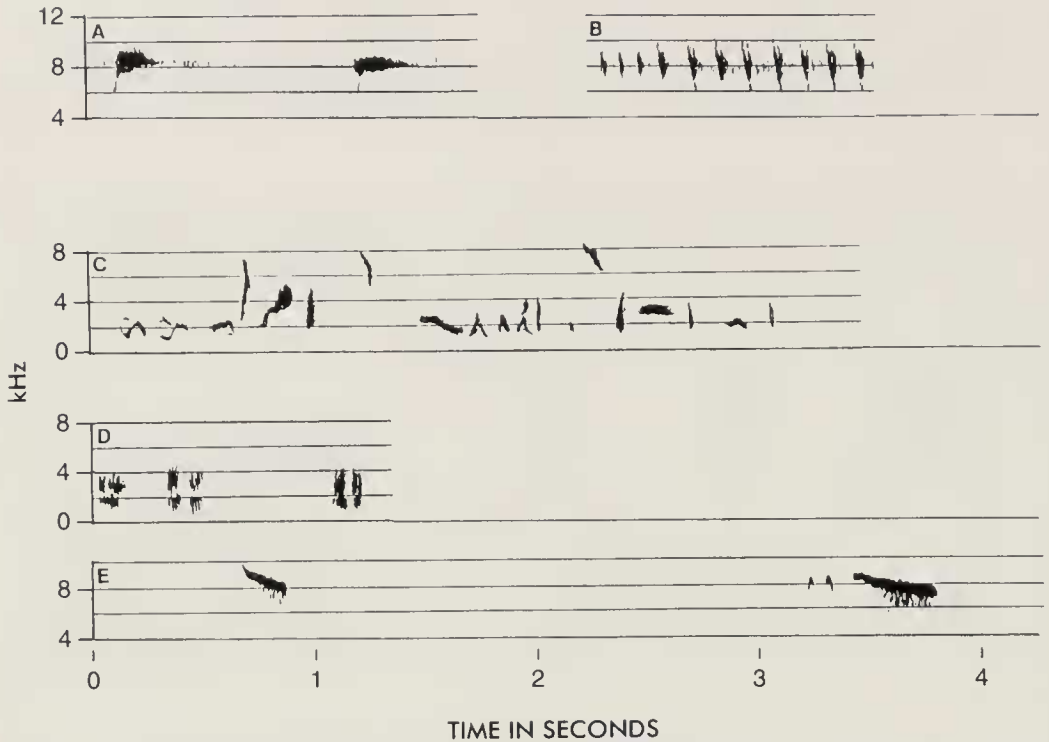


FIG. 2. Vocalizations of *Spindalis dominicensis* (see text).

The Bahamas.—Of the two forms of *Spindalis* found in the Bahamas, we know of neither a description nor a recording of the vocalizations of *townsendi* of the northern Bahamas.

Brudenell-Bruce (1975) wrote of *zena* on New Providence: “the song at the beginning of the season is a weak twittering, but it becomes more vigorous and varied as the summer progresses. Though uninteresting from a distance, it is surprisingly sweet and melodious from close to. Usually sings from a high perch, often the very top of a tree: also in flight, when a male flies from the topmost point of a pine or casuarina, circles round with slowly beating wings, in full song, and then dives down to the same or another perch. . . There is a lyrical subsong, so soft as to be almost inaudible. The call-note is a loud ‘seeip’. Small flocks keep up a soft ‘tit-tit-tit’ or ‘si-si-sit’, often hard to locate.”

The description by Brudenell-Bruce is the only report we have seen of a flight song in *Spindalis*, although some use fast calls in flying off. We have no recording of the song type he called a “lyrical subsong”, probably a female.

Tape recordings were obtained from the Cornell Laboratory of Ornithology of two individuals of *zena* on New Providence. In the first, lasting 2 min., there was a series of 17 short songs, each from 1.5 to 3.5 sec. in length, alternating with 2 to 6 sec. pauses. In sonograms of three of the short songs (Fig. 3A,B,C) most of the sounds were thin, squeaky, de-

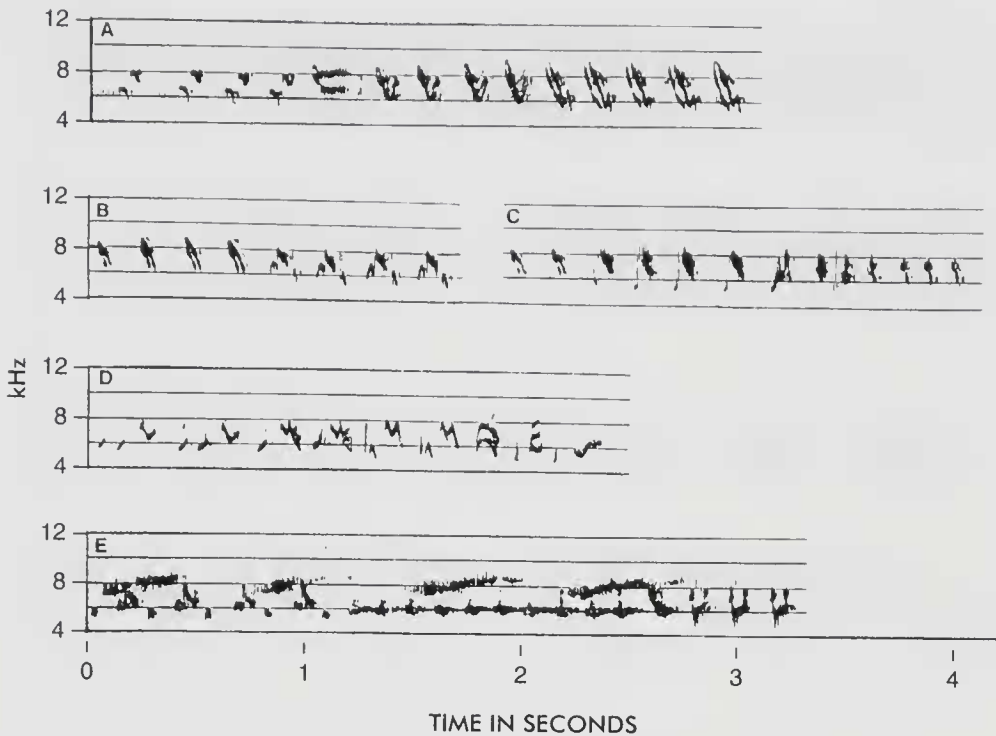


FIG. 3. Vocalizations of *Spindalis zena zena* (see text).

scending-pitch “slurs” along with two to four note syllables. Although there were several different types of vocalizations, they were each given with little change and without any resulting rhythmic pattern. One (Fig. 3C) showed a slight increase and decrease in intensity.

Sonograms were made from a 3 min. 45 sec. song session from a second individual, of four short songs included in that session (Fig. 3D,E, and Fig. 4A & B). In the latter two, the second line is a continuation of the first line in that sonogram. This individual’s singing was similar to that in Figs. 3A to C in having short songs, short pauses, and grouping of a few different syllables, each replicated a few times. The second bird differed in using more complicated syllables and particularly in using them to make rhythmic groupings. The versatility of song types is again evident, creating new syllables in each short song, not duplicating exactly any previous syllables.

In one short song (Fig. 3E) sounds around 8 kHz and others around 6kHz suggest that this is a form of “duetting”, from a double syrinx. This is also evident in another section from the same song (Fig. 4A), to be discussed below.

Cuba.—Songs from the birds in Cuba are very thin, high-pitched notes, which might be confused with those of the Cuban Bullfinch (*Melopyrrha nigra*). Among the three birds whose songs were recorded, each had a different set of notes, phrases, and patterns of delivery. A male used the

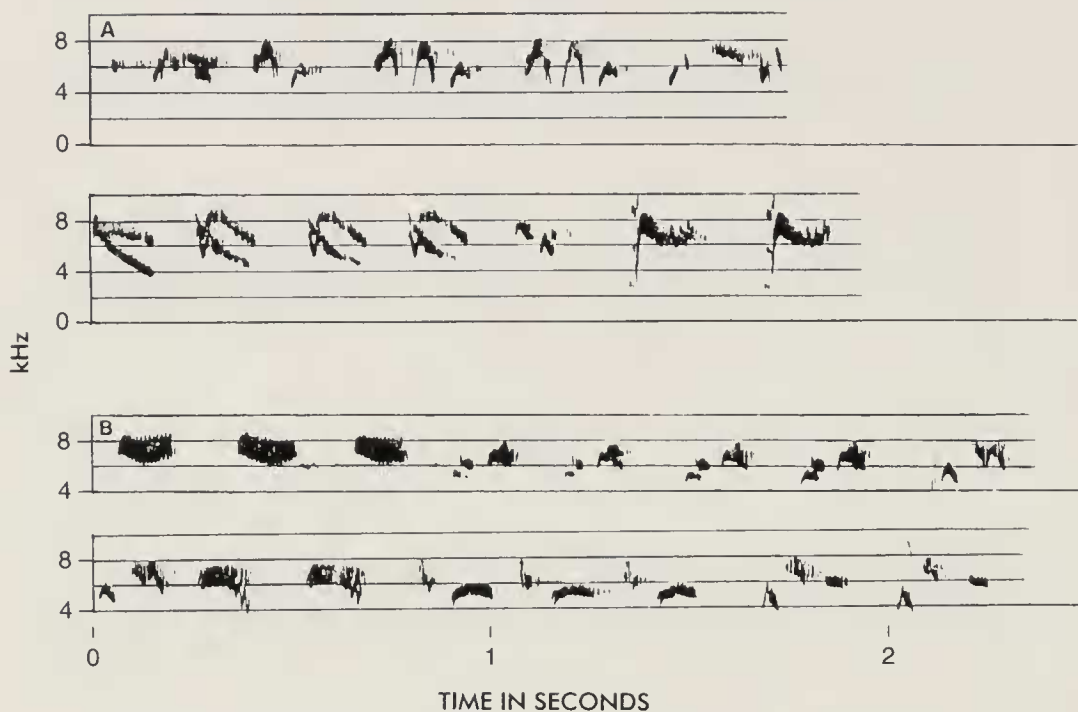


FIG. 4. Vocalizations of *Spindalis zena zena*, continued (see text).

short song, short pause pattern (Fig. 5B), delivering 17 short songs in a 37 sec. series with similar phraseology and rhythmic form.

A second bird, of undetermined sex, sang hidden in dense undergrowth, using 6–7 sec. songs alternating with 4–5 sec. pauses (Fig. 5A). It used everchanging, sibilant, thin, discrete notes, without any clear rhythmic form. A fast twitter is found in the middle of the area shown.

In the third bird, the source was again not in view, but this is a “whisper song” type of performance (Fig. 5F), believed to be from a female. It used a less common low frequency, ca. 2 kHz, initially with groups of similar syllables of notes during an 11 sec. song session. The sonogram is from a tracing of the original, which included a heavy chorus of sounds from amphibians and insects, and the high complexity in the 3rd and 4th secs. is of uncertain sources; a second tanager may have joined in for a duet, and the marks over 8 kHz may be from an insect!

Three males are responsible for the additional calls here. The weak “tsee” (Fig. 5C) was later given as a double “tsee tsee” covering less than 0.2 sec., A more intense “chip” (Fig. 5D) was used during feeding activities, and the more prolonged “see” (Fig. 5E) was used in a long series, prior to the start of a song session.

Jamaica.—Previous authors have not been impressed by the vocal performances of *Spindalis* in Jamaica. Gosse (1847) wrote “during flight, a low sibilant note is uttered; but it is usually a silent bird.” Lady Taylor

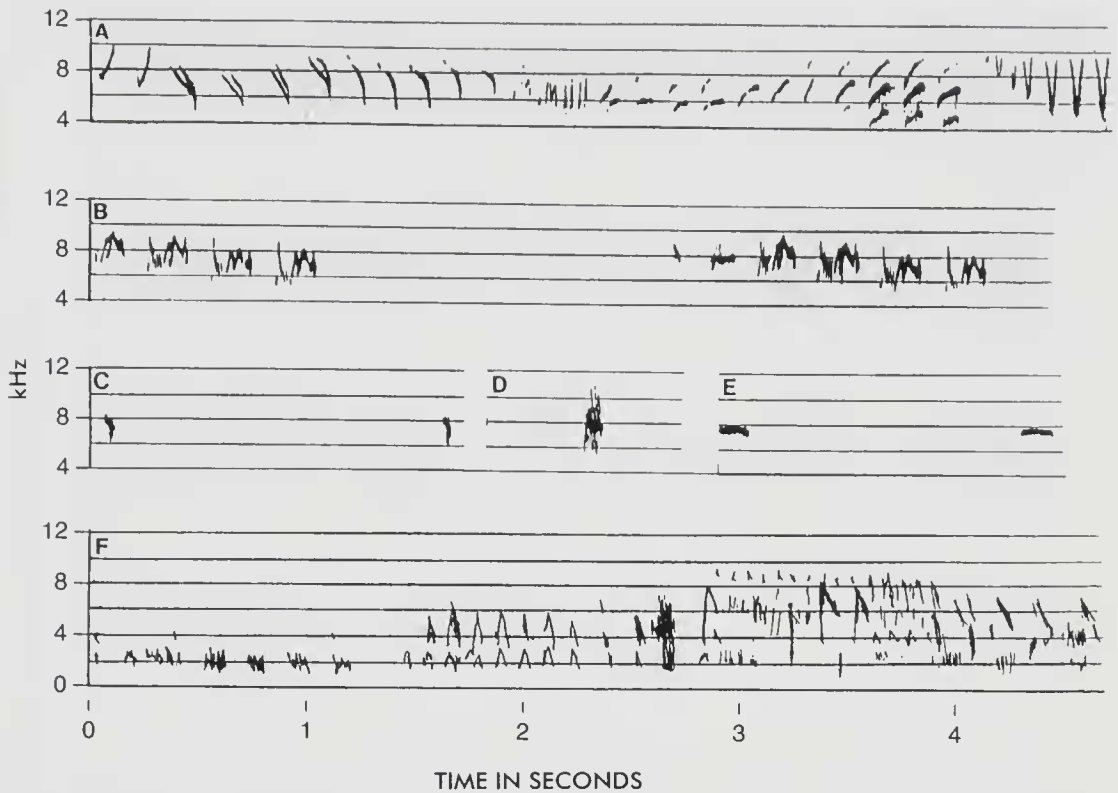


FIG. 5. Vocalizations of *Spindalis zena pretrei* (see text).

(1955) described “a crowd of as many as eight or ten of these beautiful birds. . .feeding with much chattering and scolding on fruits of a single tree. . .like many other tanagers it has no true song.” Jeffrey Smith (1956), a lifelong resident of Jamaica, wrote of *Spindalis* “It is no songster and both the male and his mate are usually silent, but in the courting season I have heard the female sing. . .When gathering material for a nest a harsh ‘chrruky’ note is uttered.” Most recently, Downer and Sutton (1990) stated that the voice of *Spindalis* in Jamaica is a “very soft ‘seep’ often given in flight, and other high, fast ‘chi-chi-chi-chi-chi’ notes.”

In contrast with the unenthusiastic reports on this tanager’s singing, Sutton, in March 1995, recorded a male with a 2 min. 20 sec. “dawn song” from high in a tree top! The distinctive performance used intense, tremulous whistles, with 7–11 syllable phraseology, like that from another male in an earlier recording (Fig. 8A). This group of whistles was given every 6–7 secs., and during the second min. of the song, several faster pulsating vocalizations were inserted, like those from another previous male recording (Fig. 7A). Also inserted were several “séaas” (Fig. 8E) in the same 8 kHz range as the song.

Our survey supports the fact that females do sing; those we taped have been classified as weak “Whisper songs.” One female in a 3 min. 40 sec.

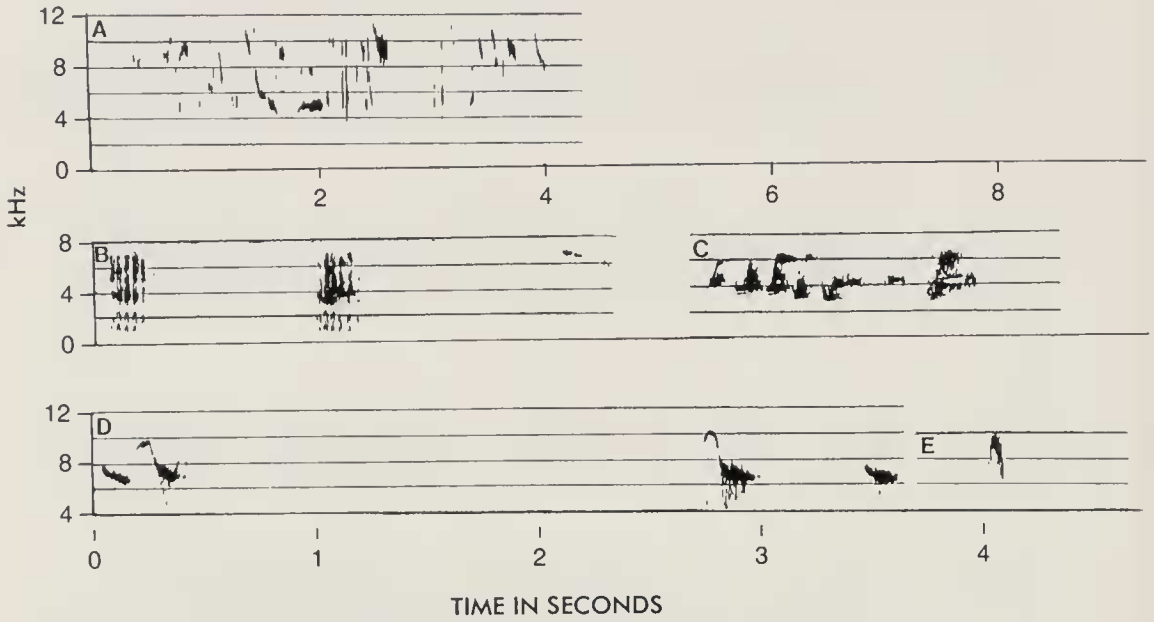


FIG. 6. Vocalizations of *Spindalis nigricephala* (see text).

performance used rhythmic short songs (Fig. 6A), some 50 times, alternating with short pauses, and included various squeaks and whistles. A second example, in this same song session (Fig. 7A) shown in an ex-

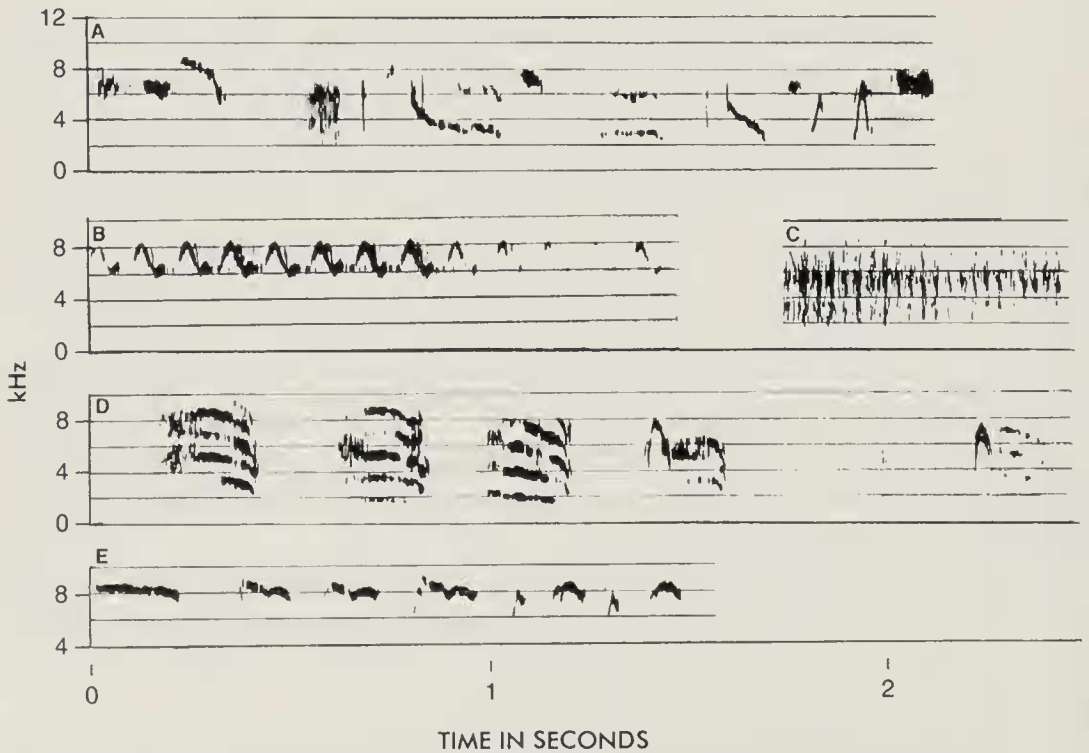


FIG. 7. Vocalizations of *Spindalis nigricephala*, continued (see text).

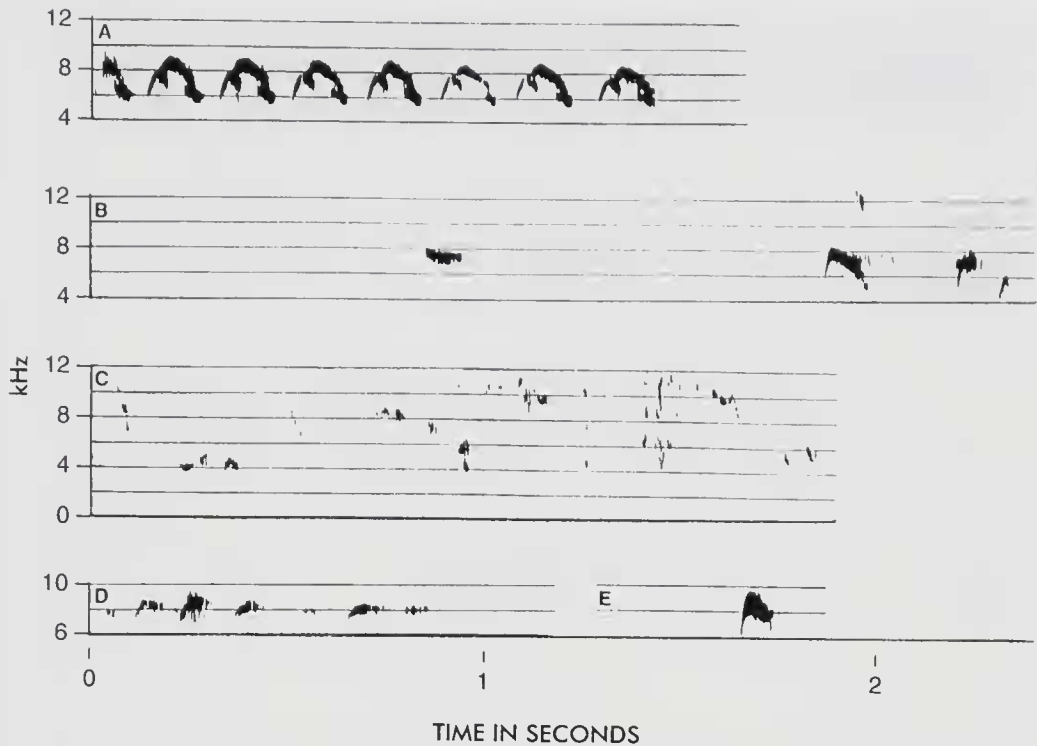


FIG. 8. Vocalizations of *Spindalis nigricephala*, continued (see text).

panded time scale, shows again the continuing variation in types of notes and phrases as well as great changes in pitch.

In a second “whisper song” from a female at Marshall’s Pen, Mandeville (Fig. 8C) there were everchanging notes and syllables in 1–2 sec. short songs, and 4–8 sec. pauses, and no rhythmic groupings. The bird was in a dense thicket, less than 0.5 m from the ground, singing so quietly that it was barely audible from a distance of 4 m, but was recorded using an 81 cm diameter parabolic reflector. Just prior to the song, it had uttered two “churrs” (Fig. 6B) and a rhythmic phrase “see seea chi lo” (Fig. 8B).

A number of miscellaneous calls are on hand, some of ours and others from outside sources, with only a few with known context, with notes accompanying the recordings. A stuttery series (Fig. 6C) appeared to have two sources, either two individuals or one individual using the two syringes; two forms of “seeps” may have been from two interacting individuals (Fig. 6D); a dry chatter (Fig. 7C) from a mostly hidden feeding group; distress notes (Fig. 7D) from a male being removed from a mist net; somewhat rhythmic high-pitched squeals (Fig. 7E) during a quick fly-off from a perch, and finally, rhythmic phrases (Fig. 8D) from a female in a mixed flock.

Among the 15 sonograms from Jamaica (Figs. 6,7,8) three are from one female (Figs. 6B, 8B & 8C), the remainder from 12 different birds.

Grand Cayman.—Of the Grand Cayman race *salvini*, Bradley (1985)

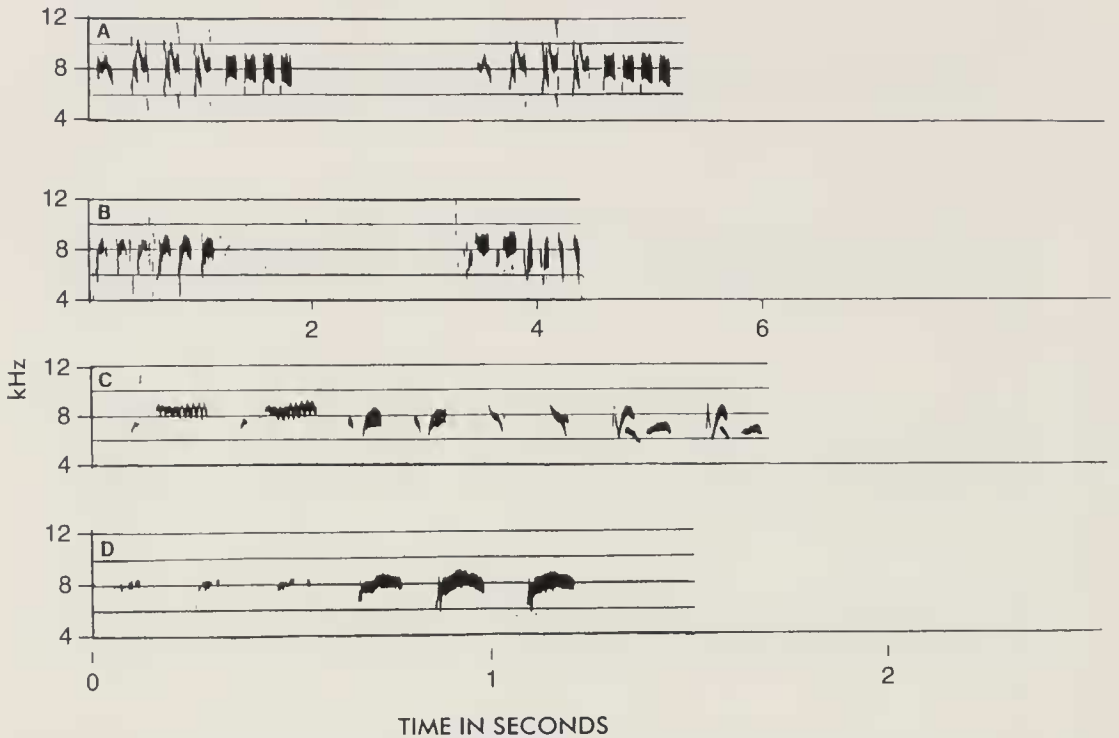


FIG. 9. Vocalizations of *Spindalis zena salvini* (see text).

wrote "Call *tweep* and a pretty mewling warble, 8 to 9 syllables rising then falling; sings constantly in spring and throughout the summer."

Recordings were obtained from two male birds, each using the short song, short pause pattern, with rhythmic phraseology. From the first, the singing emphasized terminal phrases or notes, as shown in three sonograms, during a 3 min. session (Figs. 9A, 10A, 10B). The first song in Fig. 9A is repeated in an expanded time sonogram (Fig. 10C) giving a clearer picture of the individual phrase structure. It is of interest that emphasis at first was in the 8 kHz range, dropping to 4 kHz in the 2nd and 3rd sonograms. A slight rise and fall in pitch was found in Fig. 9A.

A second bird, singing sporadically over a 3 min. period, kept inventing new notes and phrases, a common practice in all but the Puerto Rican populations, introducing them as duplicate or triplicate phrases (Fig. 9B, C, D). In the last, with the extreme loudness change, it may be that the bird turned, singing "away from" to "toward" the recordist, or else it was changing from a weak to a loud delivery. In the second song example (Fig. 9C), this pattern may be the "mewling warble" of Bradley's description above.

Cozumel Island, Quintana Roo, Mexico.—Ludlow Griscom spent three days in February 1926 on Cozumel Island, and reported (Griscom 1926) that he "did not find the present species [which he called *Spindalis benedicti*] at all common . . . It was not in song and not breeding, however,

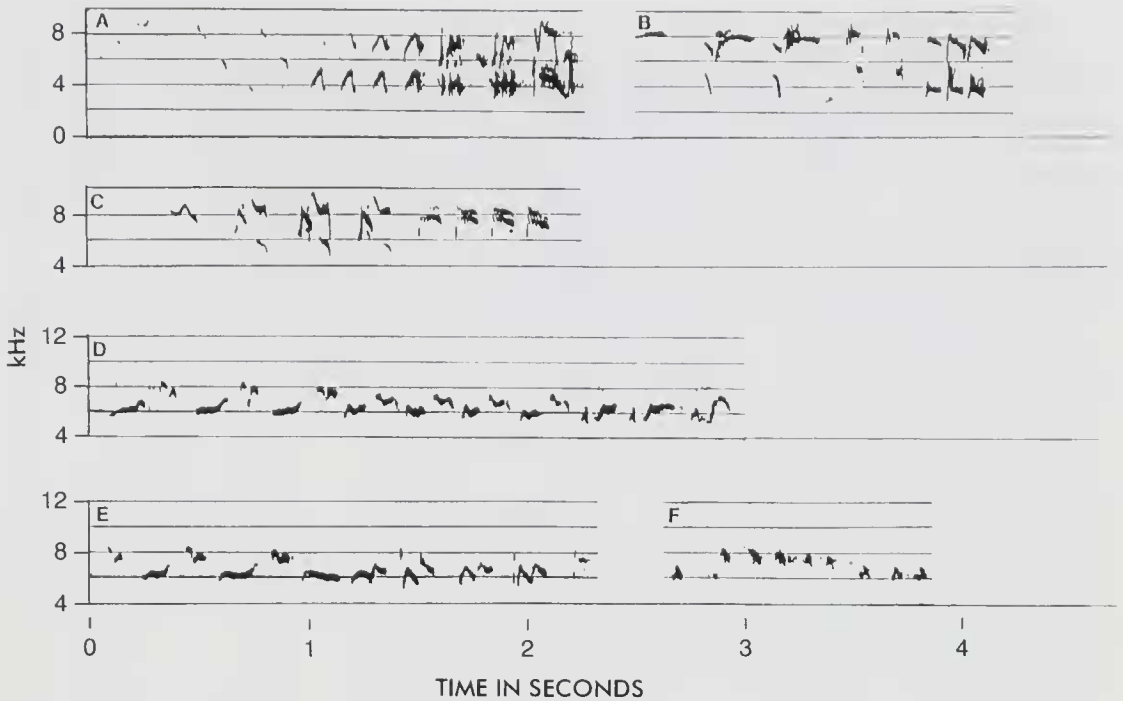


FIG. 10. Vocalizations of *Spindalis zena salvini* continued (A, B, C), and *S. z. benedicti* (D, E, F; see text).

which may in part account for its apparent scarcity.” Griscom must have been looking in the wrong habitats, as Parkes and his colleagues had no difficulty in finding non-breeding flocks of *Spindalis* on Cozumel in January and November 1965, and there is no evidence of major habitat changes on Cozumel between 1926 and 1965. Griscom described “the call-note” as “a weak, reedy lisp, suggesting notes of various species of *Chlorospingus*.” Edwards (1972) described the song of *benedicti* as “an extremely high-pitched, chipping, chattering series of notes.” Howell and Webb (1995) characterized the song as “a high, thin, twittering *tsi-si-tsi-si-si-i-tsi-si-si-i si-i*, with increasing intensity. Calls a high, thin to slightly shrill *tssi* and *tssi-ssi-ssi*, suggesting a *Turdus* flight call.”

Only one territorial song performance was available from Cozumel Island. This is a 1 min. 38 sec. session, with 2 to 4.5 sec. short songs, alternating with 3-4 sec. pauses. The songs were rhythmic and almost every different syllable appeared in duplicate, triplicate, or more replications (Fig. 10D, E).

It is of interest that the two songs, as well as most of the other 12 songs in this performance, had similar phraseology in the first second of the song, each continuing with its own variations.

In a second recording, a male used “short spurts of calls” (Fig. 10F) when displaying in flight to another bird. There were also noises from wing and tail feathers beating on air, not detected in the sonogram.

Vocalizations: discussion.—A review of the sonograms shows wide variations in many factors, including pitch, speed of delivery and types of notes or of complex syllables or phrases. We lack any long time-period tapes, e.g., 1–2 years, from any one individual, in a far from complete tape collection. Only one song series was obtained from Cozumel Island (Fig. 10D, E), and only two individuals from the Bahamas; the first (Fig. 3A, B, C) and the second (Fig. 3D, E, & Fig. 4A, B), both from *S. z. zena* and none from *S. z. townsendi*. The tapes assembled, however (Table 3), from male songs in seven locations, have given us some insight into the inter-island relationships.

One of the most distinctive male vocalizations is from Jamaica, evaluated from selected sonograms, during a recently recorded dawn song (Table 3, Figs. 8A and 7B). These are not like any other vocalizations heard or taped from other populations of *Spindalis*, supporting separate species designation for *nigricephala*. In addition, two whisper songs from females in Jamaica (the first, Figs. 6A, 7A; the second, Fig. 8C) are each quite different from whisper songs from females in Hispaniola (Fig. 2C) and Cuba (Fig. 5F).

A second distinct vocalization from males, heard in Puerto Rico (Table 3, Fig. 1A), uses short notes in both 7 kHz and 9 kHz pitch levels, to form a rhythmic song pattern. This is repeated, accurately and regularly, as a dawn song, and often at other times of day. Additional information on this population was provided by Dr. Joseph Wunderle, Jr. (in litt.), who stated that he had never heard the “high-pitched, fast warble” type of singing from Stripe-headed Tanagers in Puerto Rico.

A third distinct male song is heard in Hispaniola, recorded in the eastern (Dominican Republic) section of the island (Table 3, Fig. 2A). The dawn song uses simple, sibilant notes, similar overall to those in Puerto Rico (above), but differing as follows: in Hispaniola the song unit uses 4 similar “seeps” at one pitch, ca. 8 kHz, whereas in Puerto Rico the unit uses nine “seeps”, of three types, rhythmically in two pitches, at ca. 7 and 9 kHz.

In contrast with the simple notes in the male songs from the three locations described above, complex syllables and changing phraseology are the rule in the Bahamas, Grand Cayman, and Cozumel Island (Table 3). The sonograms are clearly different visually, as well as in hearing songs in the field. Although we do not have numerous recordings, those figured here are believed to be typical in each population.

The fourth population different from the Jamaica, Puerto Rican and Hispaniolan *Spindalis* in its vocalizations is that in Cuba (Table 3). This has complex syllables like those in the Bahamas, Grand Cayman, and Cozumel, but repeats the same syllable type instead of having ever-chang-

TABLE 3
 REPRESENTATIVE VOCALIZATIONS FROM FIGS. 1–10 CURRENTLY CONSIDERED TO BE MALE TERRITORIAL SONGS

Country	Figure	Comments	Location, date, recordist
Puerto Rico	1A	The song unit is 3 sets of these 3 syllable phrases given rhythmically and repeated every 6–7 secs.	Maricao, 20 Apr 1962 G. B. Reynard
Dominican Republic	2A	The song unit is 4 of these notes, closer together, in a rhythmic pattern, paraphrased (Wetmore 1931) as "tsee see see see"; confirmed by J. Wunderle, Jr. (in litt.).	Cotui, 8 Mar 1969 G. B. Reynard
Jamaica	8A, 7B	Two examples of the fast, intense, pulsating warbles during an early morning treetop song.	Hardwar Gap, 16 May 1995 R. L. Sutton
Bahamas (New Providence)	3A, B, C	Three parts of a short song, short pause delivery; fast, non-rhythmic, frequent syllable changes, given in a more or less "recitative" manner.	Prospect Ridge, 28 May 1971 P. A. Dean & P. P. Kellogg
Cuba (Pinar del Rio Prov.)	5B	Part of a short song, short pause session, with repeated use of the same phrase pattern (a second individual of undetermined sex [Fig. 5A] used ever-changing notes).	La Guira, 5 May 1976 G. B. Reynard
Grand Cayman	9A, 10A, B	Four rhythmic short songs with simple notes and complex syllables and terminal note group emphasis.	Georgetown, 3 June 1969 G. B. Reynard
Mexico (Cozumel Is.)	10D, E	Two of 13 short songs, most of which used the same initial notes, then all new, often repeated, low-higher syllables.	El Cedral, 20 Mar 1979 R. B. Waide

ing syllables. We have only this one male vocalization (Fig. 5B), and it follows the short song, short pause pattern.

Although the Puerto Rican and Hispaniolan territorial songs were clearly different, as described above, one call was found to be common to both islands. This was the “twitter” (Puerto Rico, Fig. 1B; Hispaniola, Fig. 2B); these are sonograms shown at two different time scales, but the sounds are essentially identical in pitch and pattern.

Another helpful report from Dr. Wunderle (in litt.) stated that *Spindalis* in both Hispaniola and the Caymans is “very different” from the birds in Puerto Rico—this referring to morphology.

Although we do not have any evidence of mimicry in *Spindalis*, its innovative phraseology, notes, or syllables challenge the degree of versatility in songs of the Northern Mockingbird (*Mimus polyglottos*)! An interesting feature of *Spindalis* songs is the ability to produce from the dual syrinx two different sounds simultaneously, an ability reviewed by Gill (1989) for several other species. Sonograms showing this feature are as follows: Fig. 3A, B, C in the Bahamas and, from a second Bahaman bird, Figs. 3F and 4A, second line; Fig. 5A from Cuba, and questionably Fig. 6C, cited earlier, which may have been from two individuals, in Jamaica.

The analyses of the vocalizations from the seven geographical areas support the morphological information on which the taxonomic arrangement proposed in this paper is based.

Natural History

The available information on the behavior, trophic niche, nesting, and foraging habits of the various forms of *Spindalis* is relatively scant. Isler and Isler (1987) assembled information on these matters from the available literature; their summaries need not be repeated here. Their taxonomic treatment follows Storer (1970) in keeping all forms of *Spindalis* in the single species *zena*, but they arrange their text into three “subspecies groups” that correspond to the three species recognized by Steadman et al. (1980). Like several other authors, they erroneously use the junior name *dominicensis* instead of *portoricensis* for what they call the “Eastern Stripe-headed Tanager.”

Comparisons of life history information as presented from the literature by Isler and Isler (1987) offer few distinctions among the taxa of *Spindalis*, and some of the apparent differences may simply be based on insufficient observations. Authors generally agree that these tanagers are primarily frugivorous, eating both berries, that are swallowed whole, and large fruits which are torn open to get at the pulp. Isler and Isler cite insectivory only for *dominicensis* and *portoricensis*. Wetmore (1927) and

Brudenell-Bruce (1975) described feeding on tender young leaves by *portoricensis* and *zena*, and the Suttons have seen *nigricephala* commonly feeding on leaves, even mature ones, in Jamaica. Wetmore and Swales (1931) mention “seeds, berries and fruits of various kinds”; the anecdotal accounts they cite all involved berries. Parkes’s observations of *benedicti* on Isla Cozumel agree with those of Wetmore and Swales who recorded *dominicensis* “traveling at times to congregate in abundance where some fruit is ripening.”

No in-depth life history studies of these tanagers appear in the existing literature, but Raúl Pérez-Rivera is presently engaged in making life history studies of *Spindalis* in Puerto Rico.

There are only a few descriptions of the nests and eggs of *Spindalis*, and none at all of some taxa. Authors agree that the nest is cup-shaped, composed of various kinds of plant materials. Bond (1936) summarized the measurements of eggs of four of the taxa as follows: *nigricephala*, 24 × 18 mm; *dominicensis*, 22 × 15 mm; *salvini*, 23.5 × 16.5 mm; and *portoricensis*, 25 × 17 mm. Wetmore (1927) measured two eggs of the latter at 23.7 × 18.2 and 24.2 × 18 mm. Pérez-Rivera (MS) gives the average measurement of 16 eggs of *portoricensis* as 23.7 × 17.3 mm. Gundlach (1893) gave egg measurements for Cuban *pretrei* as 22 × 15 mm. Despite the much larger body size of *nigricephala*, there is very little difference in egg size among these taxa.

Egg color is highly variable according to Bond (1936): “pale bluish green, marked with pale grayish brown and more or less scrawled with black about the larger end, or spotted chiefly about the larger end with brown, or brown and lilac, or heavily spotted, scrawled and marbled with various shades of brown and lavender.” Unfortunately, it is not clear whether the variation described by Bond is within a single taxon or for the whole group collectively. Gundlach (1893) described the eggs of *pretrei* as white with isolated spots, the larger darker, the smaller brown. Ogilvie-Grant (1912) described the eggs of *nigricephala* as follows: “In two eggs the ground-color is greenish-white heavily marked and blotched all over with burnt-umber and with underlying spots and blotches of paler greyish-brown, the markings being thickest toward the larger end, where they almost obscure the ground-color . . . In a third egg the markings, which are much smaller and less numerous, are reddish-brownish and reddish lilac.” The only recent description of egg color in *Spindalis* that we have seen is that of Pérez-Rivera (unpubl. data), writing of *portoricensis*. He agrees that the color and pattern of markings is highly variable, which makes it clear (as Bond did not) that this variation exists within a single island population as well as across the genus *Spindalis*. It would be necessary to examine large numbers of eggs of all of the taxa to

determine whether geographic variation transcends individual variation in egg color.

Taxonomic Conclusions

To review the vocal evidence, the recordings of Reynard (1969, 1981) indicate that the morphological distinctness of Puerto Rican *portoricensis* and Hispaniolan *dominicensis* is reflected in the differences in their vocalizations. The populations of the *zena* group (including *pretrei*, *townsendi*, *salvini*, and *benedicti*) have the most elaborate songs, that of *portoricensis* is less elaborate, and *dominicensis* even less so. The Jamaican *nigricephala* has a rattling note unique in *Spindalis*, and flight song has been described only for Bahaman and Cozumel birds; the observations of Brudenell-Bruce were made on New Providence and thus refer to *zena*.

After consideration of all available comparative data on measurements and weights, color and pattern (especially of females), voice, and distribution, we believe it is unrealistic to regard all forms of *Spindalis* as comprising a single species, *S. zena*. The A.O.U. Check-list (1983) mentions (p. 652) that "some authors have suggested that three species should be recognized, *S. dominicensis* (Bryant, 1866 [error, = 1867]) from Hispaniola, Gonave Island and Puerto Rico, *S. nigricephala* (Jameson 1835) from Jamaica, and *S. zena* in the remainder of the range . . ." This suggestion was probably taken from the footnote comment of Bond (1956), who listed all *Spindalis* as races of *zena*, but stated that the three-species treatment might be "more satisfactory."

The treatment we recommend is essentially that of Bond (1945), but with four species constituting a superspecies (although Bond did not use the latter word). The taxa are as follows (plumage characters are given earlier in this paper and measurements on Table 1):

Spindalis zena (Linnaeus), 1766

NORTHERN STRIPE-HEADED TANAGER,

with five subspecies as follows:

Spindalis z. pretrei (Lesson), 1831

Tanagra Pretrei Lesson, Cent. Zool., 1831, p. 122 (Brésil; error, = Cuba).

Synonym: *Spindalis pretrei pinus* Bangs and Zappey, Amer. Nat. 39, 1905, p. 213 (Santa Fé, Isle of Pines).

Inhabits Cuba, the Isle of Youth (formerly Isle of Pines), and numerous keys off Cuba, including Cinco Leguas, Conueco, Francés, Las Brujas, Santa María, Guillermo, Coeo, Paredón Grande, Romano, Guajaba, and Sabinal on the north coast, and Cantiles on the south coast. The color characters of the alleged race *pinus* from the Isle of Pines prove to be based on seasonal variation and the measurement differences are trivial.

Spindalis z. salvini Cory, 1886

Spindalis salvini Cory, Auk 3, 1886, p. 499 (Grand Cayman)

Endemic to the island of Grand Cayman (not yet recorded from any other island in the Cayman group).

Spindalis z. benedicti Ridgway, 1885

Spindalis benedicti Ridgway, Proc. Biol. Soc. Washington 3, 1885 (March), p. 22 (Cozumel [Island]), Yucatan.

Synonym: *Spindalis exsul* Salvin, Ibis 1885 (April), p. 189 (Cozumel Island).

Endemic to the island of Cozumel, Quintana Roo, off the east coast of the Yucatán Peninsula, Mexico.

Spindalis z. townsendi Ridgway, 1887

Spindalis zena townsendi Ridgway, Proc. U. S. Nat. Mus. 10, 1887, p. 3 (Abaco).

Inhabits Grand Bahama, Great Abaco, Little Abaco, and Green Turtle Cay islands in the northern Bahamas.

Spindalis z. zena (Linnaeus), 1766

Fringilla zena Linnaeus, Syst. Nat., ed. 12, 1766, p. 320 (Bahama Islands = New Providence).

Inhabits the central and southern Bahama Islands, from the Berry Islands south to Great Inagua, and Providenciales (only) in the Turks and Caicos Islands (Buden 1987).

Spindalis portoricensis (Bryant), 1866

PUERTO RICAN STRIPE-HEADED TANAGER

Tanagra portoricensis Bryant, Proc. Boston Soc. Nat. Hist. 10, 1866, p. 252 (Puerto Rico).

Endemic to the island of Puerto Rico.

Spindalis dominicensis (Bryant), 1867

HISPANIOLAN STRIPE-HEADED TANAGER

Tanagra dominicensis Bryant, Proc. Boston Soc. Nat. Hist., 11, 1867, p. 92 (Southeast Haiti).

Endemic to the island of Hispaniola and adjacent Gonave Island. Dod (1978) states that there is geographic variation in color in the Dominican Republic, but we have not had the opportunity to investigate this.

Spindalis nigricephala (Jameson, 1835)

JAMAICAN STRIPE-HEADED TANAGER

Tanagra nigricephala Jameson, Edinburgh New Philos. Journ. 19, 1835, p. 213 (Jamaica).

This species is endemic to the island of Jamaica. Hellmayr (1936) gave *S. bilineatus* Jardine and Selby, 1837, and *Tanagra zenoides* Des Murs, 1847, as synonyms; we have not checked these references, as both names are junior to *nigricephala*. Hellmayr also stated that *Fringilla cana* Gmelin, 1789, might be an earlier name for this species, in which case it would replace the junior *nigricephala*. However, Hellmayr found discrepancies in the descriptions on which Gmelin's name was founded and consequently declined to adopt the latter.

DISCUSSION

To some extent, the sequence of species and subspecies adopted is arbitrary. There is no evidence on which to base conjecture as to the

characters of the ancestral *Spindalis*. The amount of differentiation can be a clue as to the length of time that the populations of individual islands have been isolated from other populations. Within the *zena* group, the populations of the Cuban keys and of the Isle of Youth have not been sufficiently isolated in time, space, or both to have differentiated from *pretrei* of mainland Cuba. The same point could be made about populations of the various Bahaman islands occupied by *zena* and *townsendi*, and in fact there is evidence for gene flow between those two subspecies. The Gonave Island population of *dominicensis* has not become differentiated.

The peripheral ranges of *zena* and *townsendi* in the Bahamas, *salvini* on Grand Cayman, and *benedicti* on Isla Cozumel suggest that all of these races of the *zena* group probably originated from invasions from Cuba. The histories of the other species are harder to hypothesize, other than that the distinctness of *nigricephala* suggests a long isolation on Jamaica. For these reasons, we place the Jamaican species *nigricephala* last in the sequence, and the polytypic species *zena* first, beginning with the probable core form, the Cuban *pretrei*. The two species with streaked females, *portoricensis* and *dominicensis*, occupy an intermediate position, but the distinctiveness of the males of both species precludes any deduction as to relationships with each other or with taxa within the genus.

Nedra Klein has studied this genus from the aspect of molecular genetics (pers. comm.) In general, her findings match ours, in that *portoricensis*, *dominicensis*, and *nigricephala* are all strongly differentiated. She found that the birds of the Bahamas diverged somewhat from the others that we include in the species *Spindalis zena*, and thus she prefers to recognize five species rather than four; the fifth species would take the name *Spindalis pretrei*, and would include *pretrei*, *salvini*, *benedicti*, and *townsendi*. However, there is no "rule" that specifies the extent of genetic differentiation required for the recognition of a taxonomic species, and the mtDNA data analyzed in so many recent papers "represent a single gene tree that is embedded in the organismal phylogeny" (Zink et al. 1995), i.e., conclusions are being drawn on the basis of comparisons of a minute fragment of the bird's total genome. In view of the strong morphological resemblances within the northern populations and the distinctiveness of the Jamaican, Hispaniolan, and Puerto Rican populations, we prefer to unite the former in a single polytypic species, *S. zena*.

The only other published study of molecular genetics in West Indian birds of which we are aware is that of Klein and Brown (1994) on the Yellow Warbler (*Dendroica petechia*). This study differs fundamentally from that of *Spindalis* in that the warbler is widely distributed on the

mainland as well as on non-West Indian islands, and its history may involve multiple invasions.

As is well known, the definition of genera in ornithology is highly subjective and subject to change with alternating popularity of "lumping" and "splitting." Bond's most recent work, the 5th edition of his field guide (1985), included 44 genera endemic to the West Indies. The recent world list of Sibley and Monroe (1990) reduces this list to 36, plus three that have only recently been combined with larger, extra-Antillean genera ("*Tolmarchus*" = *Tyrannus*, "*Lamprochelidon*" = *Tachycineta*, and "*Mimocichla*" = *Turdus*). These genera can be divided into several categories. Of these, 13 are monotypic genera containing a single monotypic species inhabiting only one island (except *Cyanophaia*, which occurs on both Dominica and neighboring Martinique). Few West Indian genera are clearly polytypic, with species status made clear by sympatry; these include *Todus*, *Margarops*, and *Loxigilla* (formerly on St. Kitts; *L. portoricensis* now extinct there). Most of the endemic genera include a single polytypic species or superspecies, with the distinction not always clear (as has been the case with *Spindalis*). The lizard-cuckoo genus *Saurothera* provides the nearest parallel to *Spindalis*, as it contains two monotypic and two polytypic species (Bond 1956); however, the morphological and vocal differences among *Spindalis* species are more pronounced than in *Saurothera*.

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EDITOR'S FAREWELL

This issue ends a decade during which I processed more than 2,000 manuscripts, published more than 8,000 pages and interacted with hundreds of referees and authors. It was an entirely positive experience and I owe the members of the Wilson Ornithological Society thanks for their generosity and support throughout my editorship.

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Finally, I thank Leann Blem for her tireless, unpaid service for the past ten years. She read manuscripts, edited my prose, typed responses to authors, selected referees, kept me organized, and generally was responsible for any success the journal may have had during the period. I am lucky, indeed, to have her for my wife, partner, and colleague.

Our goal throughout our tenure was to move the journal a bit ahead of its status when we assumed the duties of editing it. I hope that you agree that we did that. Many thanks.

C. R. Blem